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The Effects of Cavity Diameter and Length on the Nesting Biology of *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae)

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Abstract.—When offered equally available trap-nests of 6, 7, or 8 mm diameter and 80, 140, or 230 mm length, *Osmia lignaria propinqua* Cresson females chose significantly more of the deepest cavities for nesting and produced 69% of their offspring in them. Proportionately more females were produced in both years in cavities of greater length and diameter. Male and female weight varied between years, cavity lengths, and cavity diameters. Mortality was not significantly related to either nest diameter or length. Nesting parameters of ten species of megachilid bees showed a positive significant relationship between both female body width and nest cavity diameter and female body length and cavity length. However, there was no relationship between female body width or length and number of cells per nest.

The cavity or wood-nesting wasps and bees (Malyshev 1935; Krombein 1967), with species found in several families (Krombein 1967; Evans and West-Eberhard 1970; Stephen et al. 1969; Gauld and Bolton 1988), represent one of the biological groupings within the Hymenoptera. These provisioning wasps and bees use natural cavities for the placement of food for rearing their offspring (Krombein 1967). Two quite different life histories exist in the group (Evans and West-Eberhard 1970). The primitive members never developed the ability to make a nest, whereas the advanced members typically make a series of cells, separated by partitions. The latter group has received much attention because of the development of the technique of "trap-nesting" (Krombein 1967) and their economic value as managed pollinators (Torchio, 1987, 1990; Bosch et al. 1992).

Evidence supporting Fisher's sex ratio theory (Fisher 1958) has come from both natural history observations on cavity nesting bees and wasps (Rau 1928, 1937; Malyshev 1935; Krombein 1967; Danks 1970, 1971; Maeta 1978) and experimental studies (Stephen and Osgood 1965; Gerber and Klostermeyer 1972; Phillips and Klostermeyer 1978; Torchio and Tepedino 1980; Cowan 1981; Freeman 1980; Tepedino and Torchio 1982a, 1982b, 1989; Tepedino and Parker 1983, 1984; Frohlich and Tepedino 1986; Johnson 1988, 1990; Sugiura and Maeta 1989; Bosch 1994). The resource quality model of cavity size (Charnov 1982) appears to be the dominant factor in the facultative sex ratios observed. Female parents of these sexually dimorphic species produce a greater proportion of progeny of the larger sex (usually females) in wider diameter cavities, and/or additional progeny of the smaller sex (usually males) in narrowed cavities. Size distribution of nest cavities available to the parent generation will shift sex ratios; more males are produced in narrow cavities, and more females are produced in wide cavities (Charnov et al. 1981).

The genus *Osmia* contains several species that have been developed as commercial pollinators of fruit crops (Maeta 1978, Torchio 1987, 1989, 1990, Bosch 1994). Much of the biological information obtained concerns the procurement and utilization of these species as pollinators. It has already been well established that both the sex ratio and the weight of individual bees of *Osmia lignaria propinqua* Cresson increased with cavity diameter (Torchio and Tepedino 1980; Tepedino and Torchio 1982a, 1982b, 1989). Bosch (1994) found that when *Osmia cornuta* Latr. was given a choice of cavity lengths for nesting they preferred the longest cavity. Maeta (1978) reported the use of an average cavity length and diameter for five Japanese *Osmia* species when given an assortment of diameter and length reeds for nesting.

Osmia l. propinqua has not been offered trap-nests of varying length (Torchio 1976, 1984a, 1984b, 1985). This paper examines the combined effects of cavity diameter and length on cavity acceptance, cavity use, offspring weight and sex, mud use for cell partitions and plugs, and mortality in *Osmia lignaria propinqua*. Also, the relationship of average female body size to average cavity selection in other cavity nesting megachilid bees is examined.

MATERIALS AND METHODS

Osmia l. propinqua individuals were obtained from trap-nests placed out during the spring and summer of 1991 and 1992 in Lake City, Modoc Co., California. Trap-nest were pine blocks drilled with 6, 7, or 8 mm holes to a depth of 80, 140, or 230 mm. Trap-nests were bundled together in groups of nine, one each by diameter and length, and 30 bundles or 270 nesting cavities were placed in each of four wooden boxes (30 × 30 × 60 cm) supported by metal fence posts 1.5 m off the ground. Trap-nest openings faced southeast. Boxes were placed out in mid March near the edge of two mixed fruit (apricots, apples, pears, peaches and plums) orchards and were from 100 to 200 m apart. With the onset of apricot bloom, trap-nests were checked daily for nesting. Completed, plugged nests were marked and dated. Trap-nests were removed in September, x-rayed, and held out-doors in Reno, Washoe Co., Nevada. In March, nests were opened and nesting information was recorded and adult bees were weighted. Temperature and precipitation were recorded daily from a station adjacent to one orchard. The duration of seasonal nesting activity was based on daylight temperatures above 15°C on precipitation free days (Torchio 1976).

Mean body lengths and widths for female *Osmia* were from Sandhouse (1939), Yasumatsu and Hirashima (1950), Rust (1974), and Peters (1977); for *Hoplitis* from Michener (1947); and for *Megachile* from Mitchell (1962).

Analysis of variance (GLM in SAS 1990) was used for all comparative analyses between years, cavity diameters, and cavity lengths and the cells per nest, mud per cell per nest, placement of first and last cell in a nest, and percentage (arcsine transformation) of mortality per nest using Type III sums of squares due to unequal observations (Cody and Smith 1991). Duncan's multiple-range test was used for multiple comparisons when analysis of variance indicated a significant difference. Female body part measurements were compared to nest dimensions using linear regression. Chi-square test and G-test (Sokal and Rohlf 1969) were used to compare trap-nest usage patterns.

RESULTS

In 1991, nesting began on 4 May: on 22 May the first nest was completed. Forty-three days (4 May to 15 June) passed to accumulate 200 hours of 15°C or greater temperatures. During that period, rain or snow (57 mm precipitation) fell on 11 days and an additional three days were below 15°C. In 1992, nesting began on 14 April: on 29 April the first nest was completed. Thirty-four days (14 April to 17 May) passed to accumulate 200 hours of 15°C or greater temperatures. During that period, rain (20 mm) fell on two days and another six days were below 15°C.

Table 1. Nests and cells produced by *Osmia lignaria propinqua* in cavities with 6, 7, and 8 mm diameters and 80, 140 and 230 mm lengths in 1992 and 1993 at Lake City, California.

	Nests			Cells			Cell
Diameter	1991	1992	Total	1991	1992	Total	Mean ± SD
				80 mm length			2.8 ± 1.2
6.0	4	3	7	14	7	21	
7.0	0	2	2	—	6	6	
8.0	1	2	3	3	10	13	
				140 mm length			5.4 ± 2.2
6.0	7	9	16	43	38	81	
7.0	6	5	11	39	22	61	
8.0	7	3	10	47	13	60	
				230 mm length			8.1 ± 4.0
6.0	12	9	21	101	55	156	
7.0	7	10	17	70	62	132	
8.0	12	9	21	117	78	195	
				Totals			
	56	52	108	434	291	725	
		Total Nest Mean ± SD 7.7 ± 3.4			Total Cell Mean ± SD 5.4 ± 3.6		

A total of 108 nests containing 725 cells were produced (Table 1). Most nests (59) and cells (482) were approximately evenly divided among the 6 mm, 7 mm, and 8 mm diameter long cavities (230 mm) (Table 1). The least nests (12) and cells (40) were in the 6 to 8 mm diameter by 80 mm short cavities. The distribution of nests was significantly different from the availability of cavities for nesting ($\chi^2 = 35.23$, df = 8, $P < 0.001$). Partitioning the nests by cavity length and cavity diameter showed no significant pattern ($G = 2.66$, df = 4, $0.75 > P > 0.50$).

The mean number of cells per nest was significantly different between the years with more cells in 1991 than in 1992 ($F = 4.51$, $P = 0.03$). Cell distribution paralleled nest distribution with significantly more cells in longer cavities ($F = 15.42$, $P < 0.001$) but a similar number of cells in all cavity diameters ($F = 0.4$, $P = 0.66$). Nests in 230 mm length cavities contained significantly more cells than did nests in 140 mm and they contained more than did nests in 80 m cavities (Table 1).

The distribution of adults by cavity length was 69% in 230 mm cavities, 28% in 140 mm cavities, and 3% in 80 mm cavities and by cavity diameter was 32% in 6 mm cavities, 30% in 7 mm cavities, and 38% in 8 mm cavities. Five hundred and forty-nine adults (317 males and 232 females) were produced (Table 2). In 1991, 312 adults (166 males and 146 females) were produced, and in 1992, 248 adults (151 males and 86 females) were produced. The distribution of males or females by cavity length was similar to the distribution of all individuals. However, the distribution of males or females by cavity diameter showed different patterns with the number of males decreasing with increasing cavity diameter (6 mm—44%, 7 mm—30%, and 8 mm—26%) and the number of females increasing with increasing cavity diameter (6 mm—17%, 7 mm—30%, and 8 mm—53%).

Both male and female weights showed a significant year by cavity length by cavity diameter interaction (males $F = 3.81$, $P = 0.02$; and females $F = 3.88$, $P = 0.02$) and were thus separated by year to ex-

Table 2. Male and female production by *Osmia lignaria propinqua* in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

	Males			Females		
Diameter	1991	1992	Total	1991	1992	Total
			80 mm length			
6.0	0	5	5	0	1	1
7.0	0	1	1	0	0	0
8.0	1	2	3	2	5	7
Total			8			8
			140 mm length			
6.0	27	26	53	7	3	10
7.0	18	13	31	16	5	21
8.0	14	4	18	13	8	21
Total			102			52
			230 mm length			
6.0	46	35	81	20	8	28
7.0	34	28	62	24	24	48
8.0	26	37	63	64	32	96
Total			206			172
			Totals			
	166	151	317	146	86	232

amine the effects of cavity length and diameter on individual weights (Table 3).

In 1991, male weights differed significantly among cavity lengths (F = 23.5, P = 0.0001), cavity diameters (F = 7.79, P = 0.001), and the cavity length by diameter interaction (F = 130.5, P = 0.01) (Table 3). Males in 80 mm length cavities were heavier than males in 140 mm or 230 mm cavities. Males in 8 mm diameter cavities were heavier than males in 7 mm or 6 mm cavities. However, in 1992 male weights were not significantly different in cavity lengths, cavity diameters, or cavity length by diameter interaction.

In 1991, female weights in were significantly different for cavity lengths (F = 6.75, P = 0.002), cavity diameters (F = 2.72, P = 0.07), and the cavity length by diameter interaction (F = 2.94, P = 0.06) (Table 3). Females in 80 mm cavities were significantly heavier than females in 140 mm or 230 mm. Females in 6 mm cavities were significantly lighter than females in 7 mm or 8 mm cavities. However, in 1992 female weights were not significantly different among cavity diameters or in cavity lengths and or their interaction.

The sex ratios based on mean weight of all males and females ranged from 1.2:1 to 1.9:1 (males: females) and were slightly different between years (Table 4). Sex ratios increased in both years with increasing cavity lengths (1.2:1 to 1.8:1) but not diameters (1992—1.6:1 to 1.9:1 and 1991—1.6:1 to 1.5:1).

The amount of mud used for each cell per nest was significantly different be-

Table 3. Mean weights and standard deviations (mg) of male and female *Osmia lignaria propinqua* produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California. * equals one individual.

	Males		Females	
Parameter	1991	1992	1991	1992
		Cavity diameter		
6.0	35.8 ± 5.7	34.2 ± 4.8	56.8 ± 11.2	54.8 ± 7.6
7.0	36.0 ± 7.3	35.1 ± 5.8	63.3 ± 9.1	59.7 ± 11.6
8.0	44.9 ± 9.5	32.6 ± 6.9	68.9 ± 12.7	61.7 ± 12.6
		Cavity length		
80	70.9*	32.6 ± 5.6	83.7 ± 5.5	53.2 ± 4.1
140	40.6 ± 6.5	35.3 ± 5.1	67.9 ± 10.2	62.2 ± 12.1
230	33.7 ± 5.2	33.4 ± 6.1	61.8 ± 11.7	60.6 ± 12.3
		Total		
Total	37.7 ± 5.1	33.9 ± 5.8	64.1 ± 10.1	60.3 ± 11.4

Table 4. Sex ratio of *Osmia lignaria propinqua* produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

Parameter	1991	1992
	Cavity diameter	
6.0	1.6:1	1.6:1
7.0	1.7:1	1.7:1
8.0	1.5:1	1.9:1
	Cavity length	
80	1.2:1	1.6:1
140	1.7:1	1.8:1
230	1.8:1	1.8:1
	Totals	
Total	1.7:1	1.8:1

Table 5. Percent mortality in *Osmia lignaria propinqua* cells produced in cavities with 6, 7, and 8 mm diameters and 80, 140, and 230 mm lengths in 1991 and 1992 at Lake City, California.

Diameter	1991	1992	Total
	80 mm length		
6.0	100.0	14.3	71.4
7.0	—	83.3	83.3
8.0	0.0	30.0	23.1
	140 mm length		
6.0	20.9	23.7	22.2
7.0	12.8	18.1	14.7
8.0	42.5	7.6	35.0
	230 mm length		
6.0	34.6	21.8	30.1
7.0	17.1	16.1	16.6
8.0	23.1	11.5	18.5
Total for:	80 mm 60.0,	140 mm 23.7,	230 mm 21.7
Total for:	6 mm 31.0,	7 mm 18.1,	8 mm 22.4
TOTAL	28.1	18.5	24.2

tween years (F = 7.32, P = 0.008) with less mud used in 1991 (mean 92.2 ± 33.2 mg versus 1992—mean 155.2 ± 95.3 mg). Mud investment per cell by cavity length and diameter was also significantly different (cavity length F = 6.46, P = 0.002, cavity diameter F = 16.4, P = 0.001). There was more mud per cell in the 80 mm cavities (163.3 ± 85.0 mg) when compared to the 140 mm (116.9 ± 77.8 mg) and 230 mm (117.7 ± 73/2 mg). The 6 mm diameter cavity nests contained less mud per cell (88.7 ± 36.9 mg) than either the 7 mm (146.0 ± 68.9 mg) or 8 mm (145.6 ± 102.9 mg).

Bees using 230 mm length cavities placed the first cell not at the bottom of the cavity but at an average of 21.4 ± 35.2 mm from the bottom of the cavity. Bees nesting in 80 or 140 mm length cavities place the first cell at the bottom of the cavity. The last cell in a nest was significantly closer to the entrance in 80 mm cavities (mean 33.7 ± 15.8 mm) than in either 140 mm (mean 50.7 ± 27.5 mm) or 230 mm (mean 75.1 ± 54.4 mm) cavities (F = 5.17, P = 0.007). For both the placement of the first and last cell in a nest, neither year, cavity diameter, or any of the interactions were significant.

The percent mortality averaged 24.2% for all cells produced and was not significantly different between years or among cavity lengths, cavity diameters, or any of the interactions (Table 5). Chalk brood (*Ascosphaera torchioi* Youssef and McManus) caused the greatest loss in 1991 (15.6%) whereas egg death or failure to hatch caused the greatest loss in 1992 (7.5%) (Table 6). Chalk brood was the overall highest mortality factor (10.9%).

Nesting parameters of ten species of megachilid bees have been reported on where they were provided with a choice of cavity lengths (Table 6). There was a positive relationship between female mean body width and mean preferred cavity diameter (Y (cavity diameter) = 1.10 + 1.50X (body width); F = 2.62, P = 0.144). The relationship became significant when *Osmia marginata* was removed from analysis (Y (cavity diameter) = −0.48 + 1.84X (body width); F = 16.6, P = 0.005). *Osmia marginata* does not place cells in a linear series in large diameter cavities, but fits cells to the cavity dimension that allows a maximum use of the space (Tepedino and Parker 1983). Female mean body length and mean cavity length also showed a significant positive relationship

Table 6. Female size and nest parameters of megachilid bees from studies where different length cavities were available for nesting.

Species	Female size		Nest characteristics			Reference
	Mean width (mm)	Mean length (mm)	Mean diameter (mm)	Mean length (mm)	Mean # of cells	
			Osmia			
imaii	3.2	8.7	5.3	9.9	8.9	Maeta 78
taurus	4.1	11.0	6.8	14.9	9.0	Maeta 78
cornifrons	3.5	9.7	5.8	14.8	8.0	Maeta 78
pedicornis	4.3	12.5	6.7	14.6	6.8	Maeta 78
excavata	3.8	10.7	6.5	15.0	7.2	Maeta 78
cornuta	4.0	12.0	8.0	17.1	4.0	Bosch 94
marginata	3.5	9.0	9.0	9.0	8.2	Tepedino & Parker 83
lignaria	3.8	11.5	6.9	18.2	6.6	present
			Hoplitis			
fulgida	3.5	9.7	6.0	8.5	4.9	Tepedino & Parker 84
			Megachile			
rotundata	3.0	8.5	4.9	7.8	6.3	Gerber & Klost. 72

(Y (cavity length) = −9.95 + 2.22X (body length); F = 17.18, P = 0.003). There was no relationship between female body width or length and the mean number of cells per nest.

DISCUSSION

Females of *Osmia l. propinqua* chose significantly deeper drilled holes in trap-nests when presented with an equal distribution of cavity lengths for nesting. These deeper holes were filled with more cells and offspring. However, females showed no preference for a particular diameter trap-nest from within the range available. This nest selection pattern was observed in both years. In similar studies, Bosch (1994) found a significant preference in *Osmia cornuta* for longer cavities for nesting (12, 15, or 21 cm, cavity diameter was 8 mm) and produced more cells in them. *Osmia marginata* Michener females preferred nest-traps in drilled elderberry (*Sambucus* spp.) stems with the longest (90 mm) and widest (9 mm) cavities (Tepedino and Parker 1983). They produce significantly more cells in them. Tepedino and Parker (1984) observed the same selection pattern in *Hoplitis fulgida* (Cresson) nesting in drilled elderberry stems. The opposite cavity usage pattern was observed in the completed nests of *Megachile rotundata* (F.) which decreased from 100% in 1.25 and 2.5 cm length cavities to 16% in 15 cm cavities (Stephen and Osgood 1965). However, nest utilization increased as cavity diameter increased from 4.0 to 6.0 mm. Gerber and Klostermeyer (1972) also found *Megachile rotundata* to use more short (4 cm compared to 8, 12 or 16 cm cavity lengths) trap-nests for nesting in a three years study. However, unlike the Stephen and Osgood (1965) results, Gerber and Klostermeyer (1972) found more cells were produced in 8 to 16 cm length cavities.

Maeta (1978) provided *Osmia imaii* Hirashima, *O. taurus* Smith, *O. cornifrons* (Radoszkowski), *O. pedicornis* Cockerell, and *O. excavata* Alfken with a broad selection of reed cavities for nesting (4 to 11.9 mm in diameter and 3 to 33 cm in length). His presentation of nesting materials attempts to represent what is most likely available to the species in nature and consequently the usage preference observed best represents the species natural usage patterns (Table 6).

The general pattern of cavity choice suggests that female size dictates her choice in both the diameter and length of cavity. This assumes that within the natural habitat there exists a variety of cavities for nesting and that females visit several cavities before making a selection. Selection of a short cavity will require finding a second or even third cavity to continue the nesting process. Selection of a long cavity simply requires the female to initiate cell construction at the "average" depth to maximize the cells or offspring produced. The bee is leaving unused cavity behind the first cell. The presence of an empty space behind the last cell was evident in only in the 230 mm long cavities. Maeta (1978) found an increasing percentage of empty spaces with increasing cavity length in all five *Osmia* species studied.

Cavity selection for nesting affects the general population structure of the species. All studies show that selection of long wide cavities allows females to produce more cells with larger offspring, and more females (Stephen and Osgood 1965, Gerber and Klostermeyer 1972, Maeta 1978, Tepedino and Parker, 1983, 1984, Frohlich and Tepedino 1986, Tepedino and Torchio 1989, Sugiura and Maeta 1989, Bosch 1994). In bee species that excavate a tunnel in a twig or stem and then construct and provision linear series of cells there is no relationship between tunnel diameter or tunnel length and the sex ratio of the offspring (Garofalo et al. 1981 for *Lithurgus,* Johnson 1988 for *Ceratina,* and Watmough 1983 for *Xylocopa*).

Why should short narrow cavities be selected by any individual females? The answer is variation both in body size and cavity size. Females are selecting from an large assortment of potential nest cavities the cavity that best matches their body width configuration. Selection of short cavities is difficult to interpret. Why should a female invest more time in foraging for and constructing cell partitions and nest plugs than in offspring production? Jayasingh and Taffe (1982) and Rust (1993) have reported on the greater cost to produce offspring in short cavities. Rust (1993) has also shown that nest plugs cost more to produce than cell partitions in *O. l. propinqua* and *Osmia ribifloris* Cresson. He suggested that a nest should contain four or more cells to equalize the extra cost of nest plug. Individuals nesting in the 80 mm length cavities were producing on average only 2.8 cells and used significantly more mud per cell than in the other cavity length nests.

The selection of a short cavity also implies that the female must spend additional time searching for a second and perhaps third cavity for nesting. Naturally occurring nest sites must be considered as clumped; beetle borings in dead trees and logs, shrubs with hollow stems, etc. This clumped distribution suggests that new site searching may be minimal. Tepedino and Torchio (1989) showed no pattern or preference for a given diameter nest when *O. l. propinqua* searched for and initiated a second or third nest.

Parasite or predator load may be a strong selective factor favoring females that select several different nest sites. Both parasite and predator build-up can become a serious problem with high mortality in commercial populations of cavity nesting bees (Torchio 1970, 1972; Stephen and Undurraga 1978; Eves et al. 1980). Females selecting one long cavity will be at a disadvantage in a high density parasite or predator site.

The overall immature mortality in *O. l. propinqua* was low, less than 30%, and is similar to other reports on cavity-nesting, non-social bees and wasps (Krombein 1967, Danks 1971, Raw 1972, Cross et al. 1975, Freeman 1977, Maeta 1978, Taffee 1979, Smith 1979, Jayasingh and Freeman 1980, Tepedino and Frohlich 1982, Tepedino and Parker 1983, 1984). The various mortality agents or factors were unrelated to either nest diameter of length in the present study. Chalk brood was the only agent to showed a substantial yearly change. Rust and Torchio (1991) also reported extreme year to year variations in chalk brood mortality within populations of *O. l. propinqua.* Tepedino and Parker (1983) reported a significantly greater mortality due to developmental failure in large diameter, long nests of *O. marginata.* They suggest the reason to be a departure in cell construction from a linear array of cells to an array of cells perpendicular to the long axis of the cavity. There was no difference in parasite or predator attacks in the various nests. In *Hoplitis fulgida,* Tepedino and Parker (1984) found significantly less mortality in the short, least used nests.

Since several species of *Osmia* and *Megachile rotundata* have been developed for commercial pollination (Torchio 1987, 1990), the choice of the appropriate cavity size is paramount to maximize pollinator production in a management strategy. The economics of producing effective commercial nest cavities requires the availability of materials and tools to manufacture the "average" cavity for a commercial population. This cavity may not be the optimum for the species. The choice of the standard length (15 to 17 cm) drill bits and the difficulties of obtaining wood with grain pattern suitable for the manufacture of "bee boards" with many straight, close, deep holes (greater than 17 cm) resulted in the production the commercial nest cavity for *O. l. propinqua* of a 7 × 170 mm paper soda straw inserted into a 8 × 170 mm hole in redwood (see Torchio 1982a, 1982b for details). This nest cavity allows for the production of sustainable populations of *O. l. propinqua* for both apple and almond pollination. My study suggests that holes deeper than 170 mm should be provided for *O. l. propinqua* for maximize its offspring production even in a commercial situation.

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